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Convergent vegetation fog and dew water use in the Namib Desert

Running title: Vegetation non-rainfall water use

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Key points

- Both fog and dew significantly increased soil water potential.
- Seven out of eight studied plant species were able to utilize fog and dew to improve their water status within the Namib Desert.
- Night fog did not affect plant water potential.
- Divergent plant and soil water potential relationships of different species indicate different pathways of plant non-rainfall water use.

Key words: Dew, drylands, fog, Namib Desert, plant water potential, soil water potential

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Abstract

Non-rainfall water inputs (e.g., fog and dew) are the least studied hydrological components in ecohydrology. The importance of non-rainfall waters on vegetation water status in arid ecosystems is receiving increasing attention. However, a clear understanding on how common plant water status benefits from non-rainfall waters, the impacts of different types of fog and dew events on vegetation water status, and the vegetation uptake mechanisms of non-rainfall waters is still lacking. In this study, we used concurrent leaf and soil water potential measurements from three years to investigate the species-specific capacity to utilize moisture from fog and dew within the Namib Desert. Eight common plant species in the Namib Desert were selected. Our results showed that both fog and dew significantly increased soil water potential. Seven of the eight plant species studied responded to fog and dew events, although the magnitude of the response differed. Plants generally showed stronger responses to fog than to dew. Fog timing seemed to be an important factor determining vegetation response, e.g., night fog did not affect plant water potential. We also found that *Euclea pseudebenus* and *Faidherbia albida* likely exploit fog moisture through foliar uptake. This study provides a first comprehensive assessment of the effects of non-rainfall waters on plant water status within the Namib Desert. Furthermore, this study highlights the importance of concurrent leaf and soil water potential measurements to identify the pathways of non-rainfall water use by desert vegetation. Our results fill a knowledge gap in dryland ecohydrology and have important implications for other drylands.

1 Introduction

Drylands cover about 40% of the global terrestrial land surface (Slaymaker and Spencer 1998). Despite the water limited conditions, drylands contribute about 40% of global net primary productivity (Grace et al. 2006, Wang et al. 2012). Non-rainfall water, particularly fog and dew, is a potentially important water source for dryland vegetation (Wang et al. 2017) since any additional source of water may have a positive impact on productivity in water-limited systems (Zhuang and Zhao 2008, Wang et al. 2010, Yu and D'Odorico 2014). Non-rainfall waters can exceed annual rainfall and could be the only water source for biota during rainless periods in many dryland systems (Wang et al. 2017). As a result, the ecophysiology of desert organisms may be geared towards obtaining and utilizing non-rainfall water (Henschel and Seely 2008). However, non-rainfall water is much less studied than rainfall because research often focuses on factors limiting rather than sustaining productivity in arid environments. As such, non-rainfall water is often not well characterized in most ecosystems (Brown et al. 2008).

Fog is defined as a ground-touching cloud or suspended water droplets reducing visibility to less than 1000 m (WMO 1992, Glickman and Zenk 2000) while dew is the condensation of water vapor on a sufficiently cooled substrate surface (Beysens 1995). Dew is typically considered scarce and negligible to plant water budgets, at the same time, dew is often sufficient to propagate some plant pathogens (Sentelhas et al. 2008). However, there is evidence suggesting that dew is not only hydrologically significant (Zangvil 1996) but also supplies up to 63% of plant water requirements in certain environments (Hill et al. 2015).

Currently, we lack an understanding on how common plants are able to harvest and utilize non-rainfall waters. We also lack an understanding on the effects of timing (e.g., morning fog vs. evening fog) as well as seasonality of non-rainfall water (e.g., summer fog vs. winter fog) on plant water use. More importantly, mechanisms by which fog and dew alleviate vegetation water stress are still uncertain (Konrad et al. 2015, Wang et al. 2017). Enhancing understanding of these aspects of fog and dew effects on plant water budgets will help in

quantifying and modeling the impacts of climate change on the non-rainfall water dependent ecosystems.

The direct impact of non-rainfall water vectors is typically confined to the upper few centimeters of the soil profile (Louw and Seely 1982, Jacobs et al. 1999, Li et al. 2018) where plants with surface roots can exploit this resource (Seely et al. 1977, Hill et al. 2015). Hence, concurrent plant and surface soil water potential measurements under different types of fog and dew conditions could be a feasible option to identify the non-rainfall water use pathways. If a plant utilizes non-rainfall water mainly through root uptake, there should be a strong correlation between plant and soil water potential for this plant; on the other hand, if a plant utilizes non-rainfall water mainly through foliar uptake, there is not necessarily a correlation between plant and soil water potential.

The Namib Desert is a coastal desert in southern Africa, stretching more than 2,000 km along the Atlantic coasts of Angola, Namibia and South Africa. The Central Namib Desert is classified as a hyper-arid environment of which the western half receives less than 25 mm of annual rainfall (Eckardt et al. 2013) but with an abundance of fog (Henschel and Seely 2008, Kaseke et al. 2017a, Kaseke et al. 2017b). Given the abundance and importance of non-rainfall waters especially fog in the Central Namib Desert, this setting provides an ideal location to study the effects of non-rainfall water on vegetation water status.

In this study we measured leaf and soil water potential to identify the species-specific response to the different non-rainfall water components within the Namib Desert. The objectives of the current study are to 1) identify species that are capable of utilizing non-rainfall water, 2) investigate whether different types of fog and dew (e.g., summer vs. winter fog, regular vs. heavy dew) as well as timing (e.g., night fog vs. morning fog) affect vegetation water response, 3) investigate the effects of fog and dew on soil water conditions, and 4) examine whether concurrent plant and soil water potential measurements can inform different vegetation fog/dew water use pathways.

2 Materials and Methods

2.1 Site Description

This study was conducted in the central Namib Desert at the Gobabeb Research and Training Centre (lat. -23.55˚, long. 15.04˚ and elv. 405 m a.s.l.). The research center is located about 60 km from the Atlantic Ocean on the outer edge of the Namib fog-zone, annual precipitation around the research center is < 20 mm (Eckardt et al. 2013). The fog zone is an area of the most visible impacts of advective fog characteristic of the Namib coast (Olivier 1995) although there are reports that other types of fog occur regularly in the Namib (Seely and Henschel 1998, Eckardt et al. 2013, Kaseke et al. 2017a). The research center is surrounded by three distinct ecosystems: the gravel plains, sand dune sea and the ephemeral Kuiseb river (Fig. 1). Typically, there are two seasons in Namibia: cool and dry winter (May to September), and hot and rainy summer (October to April). Almost all the annual precipitation (> 99%) occur during the summer season (Lu et al. 2016b) but fog occurs in both seasons. *Acacia erioloba*, *Euclea pseudebenus*, *Faidherbia albida*, *Salvadora persica* and *Tamarix usneoides* grow in the riverine systems (Schachtschneider 2010); *Acanthosicyos horridus* and *Tamarix usneoides* on the dune sands; and *Calicorema capitata* and *Acacia erioloba* on the gravel plains.

Figure 1 here

2.2 Field measurements and data analyses

All field measurements were conducted within the vicinity of Gobabeb Research and Training Centre during four field campaigns between May 2015 and June 2017 (June 2015, June 2016, December 2016 and June 2017), including both summer (December) and winter (June)

measurements. Eight common plant species (*Acacia erioloba, Acanthosicyos horridus* (!nara), *Calicorema capitata, Euclea pseudebenus, Faidherbia albida, Salvadora persica, Stipagrostis sabulicola* and *Tamarix usneoides*) within the Namib Desert with different life forms (e.g., grass, shrub, tree) were selected for this study. *Salvadora persica, F. albida, A. erioloba, E. pseudebenus* and *T. usneoides* are widespread species that grow in the riparian area. *Acanthosicyos horridus* and *S. sabulicola* grow on river banks and the base of dunes. *Calicorema capitata* and the occasional *A. erioloba* occur on the gravel plains. Leaf water potential measurements were conducted before sunrise (i.e., 05:00 am - 06:00 am local time). The Model 1000 Pressure Chamber Instrument (PMS Instrument Company, Albany, OR, USA) was used for leaf potential measurements. During the June 2016 and June 2017 field campaigns, soil water potential measurements were also conducted concurrently with leaf water potential measurements using the Decagon WP4C Dewpoint Water Potential Meter (Meter Group, Inc. Pullman, WA, USA). Five locations were selected for soil water potential measurements with three replicates at each location: open area, riparian area, under *A. horridus*, *C. capitata* and *S. sabulicola*. Soil samples were taken from the top 2 cm using the cup holders designed for the Dewpoint Water Potential Meter. For the four vegetated areas, soil samples were taken under the vegetation canopy but away from the vegetation stems. The collected soil samples were sealed in the cup holders and placed in a cooler box before measurements (i.e., measurements were made within two hours of sampling). To better understand the relationship between soil gravimetric water content and soil water potential in the studied systems, water retention curves were created for three types of soils: soils from open areas around Gobabeb, under *A. horridus* and dune sands. The water retention curves were determined by measuring the water potential values - using a water activity meter, WP4C Dewpoint Water Potential Meter (Meter Group, Inc. Pullman, WA, USA) and gravimetric moisture content using field collected soil samples from these locations in the laboratory setting. Because moisture inputs from fog and dew quickly dissipate and evaporate during the day and the desert environment resets itself every day within the Namib Desert, we considered each day's measurements independently. During each field campaign, all the moisture events (i.e., fog or dew) were pooled together and all the ambient days (i.e., the days without moisture events) were pooled together for statistical analyses. The fog and dew occurrences were monitored through observations during the field campaigns. Most fog events during these observation periods (four field campaigns) occurred in the morning between 4 am and 8 am and only one fog event occurred at night (9 pm - 11 pm in June 2017). Dew was collected using clean paper towels from a car, similar to the method described in Beysens et al. (2016). Based on previous field experiences, a dew event with around 15 ml water collected was considered as a regular dew event and larger than 30 ml water collected was considered as a heavy dew event in this study. Earlier studies show that there are potential differences between the amounts of dew formed on artificial surfaces and the amounts of dew formed on the soil surface (Agam and Berliner 2006). In this study, the main purpose was to differentiate heavy vs. regular dew events using the same collecting methodology, so the possible amount differences between soil and artificial surfaces would not affect data interpretation.

The t-test was conducted to test significance of the differences between ambient and fog/dew conditions regarding both plant and soil water potential. Pearson correlation coefficients were calculated to test the correlation between plant and soil water potential. All the statistical tests were conducted using R (RStudio ver. 1.0.153, 2017). The significance level was set as $\alpha = 0.05$ for all the tests.

3 Results

3.1 Vegetation responses to fog

Most plant species responded to fog events except *C. capitata*, which was not responsive to any of the fog events. The other seven species *A. erioloba, A. horridus, E. pseudebenus, F. albida, S. persica, S. sabulicola* and *T. usneoides* responded to fog events at least once during the four field campaigns. Specifically, in June 2015 we examined four species, of which *A. erioloba, A. horridus* and *T. usneoides* responded to fog events while *E. pseudebenus* did not respond (Fig. 2). The water potential of *A. erioloba, A. horridus* and *T. usneoides* increased from -2.50 MPa, -0.89 MPa and -2.23 MPa under ambient conditions to -1.50 MPa, -0.066 MPa and -1.50 MPa after fog, respectively. In June 2016, out of the eight species we examined, only *C. capitata* and *F. albida* did not respond to fog events (Fig. 2). The water potential of *T. usneoides, E. pseudebenus, S. persica, A. horridus, A. erioloba* and *S. sabulicola* increased by 1.63 MPa, 0.72 MPa, 0.50 MPa, 0.68 MPa, 1.76 MPa and 0.88 MPa, respectively. In June 2017, out of the seven species we tested, only *C. capitata* did not respond to the fog events (Fig. 2). The water potential of *F. albida, T. usneoides, E. pseudebenus, S. persica, A. horridus, A. erioloba* and *S. sabulicola* increased by 1.06 MPa, 1.05 MPa, 0.48 MPa, 1.00 MPa, 1.00 MPa and 0.57 MPa, respectively. In December 2016 (summer fog), out of eight species examined, *T. usneoides, S. sabulicola, A. erioloba* and *A. horridus* responded to fog (Fig. 3). The water potential of *T. usneoides, S. sabulicola, A. erioloba* and *A. horridus* increased by 0.77 MPa, 0.68 MPa, 0.93 MPa and 0.64 MPa, respectively. None of the studied species responded to night fog events (June 2017) and their respective water potentials were the same between ambient and fog conditions (Fig. 4).

Figure 2-4 here

3.2 Vegetation responses to dew

Different species differed in their responses to dew events. Only *A. erioloba* and *E. pseudebenus* responded to a regular dew event in June 2016. The water potential of *A. erioloba* increased from -2.76 MPa under ambient condition to -2.38 MPa after the dew event. The water potential of *E. pseudebenus* increased from -3.64 MPa under ambient condition to -3.15 MPa after the dew event (Fig. 5). *Acanthosicyos horridus, S. sabulicola, A. erioloba* and *T. usneoides* responded to a heavy dew event in June 2016. The water potential of *A. horridus, S. sabulicola, A. erioloba* and *T. usneoides* increased from -0.83, -1.30, -3.00 and -2.76 MPa under ambient condition to -0.08, -0.60, -1.63 and -1.43 MPa after the heavy dew event, respectively (Fig. 6). Therefore only *A. erioloba* responded to dew events regardless of the magnitude of the event. *Euclea pseudebenus* responded to regular dew events but not the heavy dew event (water potentials were higher under the heavy dew event than under ambient condition but not significant), this result maybe an artifact due to the very small sample size (n =3) for the heavy dew event sampling for *E. pseudebenus*.

Figure 5-6 here

3.3 Soil water potential responses to non-rainfall waters

Soil water potential was significantly higher after fog and dew events than under the ambient condition in both 2016 and 2017. In 2016, the ambient soil water potential was between -96.62 MPa and -65.01 MPa across five locations. The water potential was between -24.29 MPa and -0.23 MPa after morning fog events, between -59.96 MPa and -41.31 MPa after regular dew events, and between -38.45 MPa and -0.56 MPa after the heavy dew event across five locations (Fig. 7). In 2017, the ambient soil water potential was lower, ranging between -149.44 MPa and -120.10 MPa across the five locations. The water potential was between -

50.29 MPa and -3.27 MPa after the morning fog events, between -60.64 MPa and -31.53 MPa after the night fog across five locations (Fig. 7). The soil water potential increases were generally higher under *A. horridus* and *S. sabulicola* than other locations for fog events (Fig. 7). The increases were also higher under *S. sabulicola* than other locations for the heavy dew event (Fig. 7). The soil water potential increases were similar across five locations for regular dew events and night fog (Fig. 7).

Figure 7 here

3.4 Correlations between vegetation and soil potential

There was no correlation between soil and plant water potential for *C. capitata* in both 2016 and 2017 (Table 1). However, the other seven species that showed responses to fog and dew had significant positive correlations between plant water potential and soil water potentials with the exception of *F. albida* and *E. pseudebenus* (Table 1). This indicates *F. albida* and *E. pseudebenus* likely take up fog water mainly through foliar uptake instead of root uptake. *T. usneoides* showed marginal significant response to soil water potential changes in 2017 and *A. horridus* showed marginal significant response to soil water potential changes in 2016 (Table 1), indicating a possible contribution from foliar/stem uptake for these two species as well.

4. Discussion

Very few studies have documented the effects of fog and dew on soil water potential. A recent study conducted within the Namib Desert showed that fog events can impact soil moisture dynamics during rainless periods and the effects can be modeled using a stochastic framework (Li et al. 2018). Current results show that soil water potential is more sensitive to fog than soil moisture since large changes in soil water potential were observed regardless of fog magnitude and fog timing. Regardless of the timing of the fog events during a day (e.g., morning fog vs. night fog), soil water potential significantly increased after such events. Soil water potential increased by about 87 MPa and 110 MPa after fog events in 2016 and 2017, respectively, an increase of almost 100%. Night fog increased soil water potential by similar magnitudes. The dew effects on water potential were smaller, but nonetheless still significant. Soil water potential increased by about 50 MPa after dew events (about 50% increase). Soil water potential increased by almost 100 MPa after heavy dew events (about 100% increase), a magnitude very similar to the fog effect. Such magnitude of changes clearly indicate that non-rainfall waters could significantly impact soil water status and potentially affect soil microbial activities and soil biogeochemical cycles as they are sensitive to soil water changes (Wang et al. 2015). The soil water potential increases were higher under *A. horridus* and *S. sabulicola* than other locations likely due to their unique canopy structures. *Stipagrostis sabulicola* represents one of the few successful perennial inhabitants of the Namib dunes and it is capable of adding biomass to the dune system when nothing else can grow. A medium-sized hummock of *S. sabulicola* was reported to be able to collect up to 5 L of fog water during one fog event (Ebner et al. 2011). *Acanthosicyos horridus* is a leafless non-succulent C_3 plant that is an efficient fog collector due to its dense and tangled canopy structure. Its green stems are grooved, bearing slender, conical spines angled to optimize directional water flow.

Vegetation non-rainfall water uses have been documented for multiple species. For example, it was shown that 28-66% of *Sequoia sempervirens* water uptake during the summer drought came from fog instead of soil water under the Mediterranean climate in California (Corbin et al. 2005). Eller et al. (2013) found that *Drimys brasiliensis* uses fog water in cloud forests. Many of these studies are from relatively humid areas and such information is still lacking from drylands where non-rainfall waters potentially play a critical role in vegetation

survival. In this study, we studied eight common species within the Namib Desert fog zone. Seven out of eight studied species showed responses to fog and dew waters, as indicated by the significant increases in their pre-dawn water potential after the fog and dew events. This suggests that non-rainfall utilization may be a common opportunistic trait for plants occurring in fog dominated systems. At the same time, different species showed different responses, likely related to the differences in their anatomical and physiological characteristics (e.g., leafy vs. leafless, C_3 vs. C_4). Ebner et al. (2011) reported that *S. sabulicola* can precipitate up to 4-5 L water per fog event due to their canopy structure (e.g., spikiness, tangled stems), which could contribute to their strong water potential responses to fog events. After fog events, the stem water potential of *A. horridus* almost reached saturation. Previous anatomical studies of the stem (Kartusch and Kartusch 2008) revealed anastomosing idioblasts, containing cucurbitacin solutions and associated with the vascular bundles. The relationship of these turgid idioblasts to *A. horridus* stem physiology is not known, but potentially they may play a role in stem-water relations. In other taxa (e.g., *Rhododendron*), it has been suggested that idioblasts in leaves could affect leaf-water relation parameters (Tulyananda and Nilsen 2017). An extensive stem-borne adventitious root system within the *A. horridus* hummock could also indicate that the plant efficiently utilizes precipitated drip water from fog (Kutschera et al. 1997). *A. erioloba* was the only species that responded to both regular dew event and heavy dew event. The physiological base of such responses requires further investigation. Our results were different from the conclusion that *A. erioloba*, *F. albida* and *T. usneoides* do not use fog water based on isotope tracing (Schachtschneider 2010). This discrepancy may be related to the time scale of interest, e.g., plants may only utilize fog water in the early morning right after fog events. In fact, a close examination of Schachtschneider (2010)'s isotope tracing calculation revealed up to 7% of fog water use by *A. erioloba*, *F. albida* and *T. usneoides*. This range is consistent with our expectation of a small contribution of fog water use for these plants; and such small percentages of fog water use may not be sufficient to be reflected in the isotope signal of plant xylem water when integrated over a long period. We found night fog (occurred between 9 and 11pm) did not affect plant water potentials, likely because plant transpiration rates and leaf conductance are low at night (relative to day time), affecting both foliar and root water uptake.

Plant roots provide the major pathway for vegetation water uptake. But foliar water uptake for atmospheric moisture, rain and fog have also been well documented (Berry et al. 2019). For example, it was shown that Coulter pine in southern California can survive on soils below permanent wilting point and it was suggested that the aerial parts of plants take up water from the atmosphere particularly at night (Stone et al. 1950). Field observations and isotope labelling in the laboratory showed the *Juniperus* can take up intercepted rainfall water during drought to improve plant water status (Breshears et al. 2008). Vegetation fog water use has been identified through foliar uptake by *Sequoia sempervirens* (Burgess and Dawson 2004) and *Drimys brasiliensis* (Eller et al. 2013). It was found that fog water taken up by leaves could be transported belowground to alleviate drought effects for *Drimys brasiliensis* in cloud forests (Eller et al. 2013). Foliar fog water uptake has also been reported in *Trianthema hereroensis*, an endemic succulent restricted to the fog zone of the Namib Sand Sea (Seely et al. 1977). In this study, we showed that woody plants, *F. albida* and *E. pseudebenus* likely take up fog water through foliar uptake because no correlation was found between plant water potential and soil water potential, however, the stem water potential of both species significantly increased after fog events. Berry et al. (2019) assembled a list of species that have been reported to take up water through foliar uptake and our study contributed two new species for possible foliar fog water uptake. Our results also indicate that concurrent leaf and soil water potential measurements could help identify plant foliar water use. Based on the positive correlations between soil and plant water potentials, root water uptake or combined root and foliar water

uptake are the likely pathways for the other five species responded to fog and dew events. In this study, soil water potentials were significantly lower than plant stem water potentials even after fog and dew events. There are several reasons that the lower soil water potentials could be biased due to the measurement procedures applied. First, the soil samples were not taken from the vegetation stem base, where soil water content has been found much higher than that of mid-canopy position (Ebner et al. 2011). By combining the soil water retention curve (Figure 8) and reported soil volumetric water content (2.2%) at the culm base (Ebner et al. 2011) as well as soil bulk density (1.59 g/cm^3) for sand dunes, we found soil water potential under *S. sabulicola* is up to -0.27 MPa after fog events. Second, even sealed, soil inside the containers does lose a small amount of water before WP4C measurements, lowering the soil water potential readings. *In situ* soil water potential measurements could be the only way to attain unbiased water potential measurements. Fine temporal resolution unbiased water potential measurements coupled with fine root distribution survey would be a good way in the future to confirm soil water uptake pathway including whether sufficient water potential gradient is established to allow plant water uptake from roots after fog and dew events.

Improvement in plant water status under fog and dew conditions can possibly result from one of the two mechanisms: inhibition of water loss and intake or absorption of water into the plant system. In this study, we mainly used predawn plant water potential to indicate improvement in plant water status, implicitly implying water intake. There are limitations in such approach. Predawn plant water potential is measured with the assumption that it equilibrates with the moist soil layer when stomata are closed (i.e., without transpiration) during the night. For most plants in the subtropical or tropical system with abundant soil moisture condition, this assumption will likely be met. However, predawn disequilibrium was reported for multiple species under dry soil condition, so is the night transpiration reported for some species (Yu et al. 2019). If any of the two conditions exist for the plants studied, then the fog and dew events can affect the plant water status through regulating transpiration and water does not need to be "used" by plants. It is not known if night transpiration may take place in any of the species we tested, nor if they may show predawn disequilibrium. In addition, if inhibition of water loss is the mechanism of plant water status improvement after fog and dew events, we would not see an increase in plant water potential and it would be less reduction in water potential during morning hours after fog and dew events, compared to non-fog/dew conditions. In fact, we observed plant water potential increases in majority of the species we considered in this study. Furthermore, if the inhibition of water loss is the mechanism of plant water status improvement after fog and dew events, in theory it should affect all the studied species from the same ecosystem. In this study, not all the studied species responded to fog and dew events. That said, all of these do not eliminate the possibility of plant water status improvement under fog and dew conditions through inhibition of water loss. Further studies are needed to clarify the underlying mechanisms for the observed improvements in plant water status after fog and dew events. Stable isotopes are powerful tracers to track plant water use across different ecosystems (Dawson and Pate 1996, Lu et al. 2016a, Zhao et al. 2016, Zhang et al. 2019). Stable isotope analyses of both non-rainfall waters and stem water at high temporal resolution would be a promising approach to examine whether improvement in plant water status after fog and dew events is caused by absorption of water into the plant system through either foliar or root uptake.

5 Conclusions

Despite the increasing attention of non-rainfall water effects on vegetation water status in arid ecosystems, we still have limited understanding on how common plants utilize fog and dew and the physiological and anatomical pathways of plant non-rainfall water use. In this study,

we used field observations obtained over four field campaigns within the Namib Desert to identify species that are capable of utilizing fog and dew waters, investigated whether different types of fog and dew as well as fog timing affect vegetation water response, investigated the effects of fog and dew on soil water conditions, and examined whether concurrent plant and soil water potential measurements can inform different vegetation fog/dew water use pathways. Eight common plant species in the Namib Desert were selected for this study. We found soil water potential is very sensitive to both fog and dew events within the Namib Desert. Morning and night fog showed similar effects on soil water potential. Seven out of eight of the studied plant species showed strong responses to fog and dew events, indicating non-rainfall water use could be a common phenomenon in the fog-dominated part of the Namib Desert. We found night fog did not affect plant water potential and plants tended to be more responsive to fog than to dew. Most species that responded to fog and dew showed strong correlations between plant and soil water potentials. However, no correlation was found between plant water potential and soil water potential for two trees, *F. albida* and *E. pseudebenus*, likely indicating that they take up fog water through foliar uptake. This study showed the strong response of plants and soil to fog and dew within the Namib Desert, emphasizing the potential importance of fog and dew in ecohydrological processes in some drylands. This study provides a first comprehensive assessment of the effects of non-rainfall waters on plant water status within the Namib Desert and significantly enhances our understanding of vegetation non-rainfall water use in such systems. Our results also show that concurrent leaf and soil water potential measurements could help identify the pathways of plant non-rainfall water use. These results have important implications in other dryland regions and fill an important knowledge gap in dryland ecohydrology.

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Table 1: The relationships between soil and plant water potential for *Calicorema capitata, Faidherbia albida, Tamarix usneoides, Euclea pseudebenus, Salvadora persica, Acanthosicyos horridus, Acacia erioloba* and *Stipagrostis sabulicola* in 2016 and 2017.

	2016		2017	
	r	p-value	r	p-value
Calicorema capitata	-0.144	0.785	0.200	0.703
Faidherbia albida	0.649	0.115	0.750	0.143
Tamarix usneoides	0.840	0.002	0.822	0.0879
Euclea pseudebenus	0.492	0.261	0.290	0.635
Salvadora persica	0.750	0.032	0.983	0.003
Acanthosicyos horridus	0.624	0.054	NA	NA
Acacia erioloba	0.933	0.001	0.855	0.030
Stipagrostis sabulicola	0.957	0.001	0.892	0.042

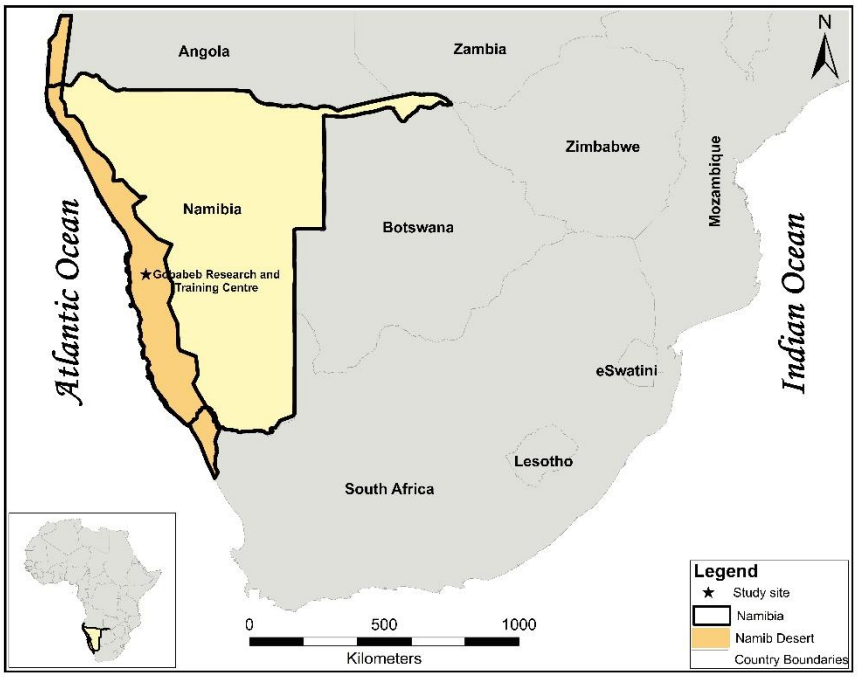

Figure 1: A map showing the location of Namibia (insert) and the study site at Gobabeb Research and Training Centre within the Namib Desert.

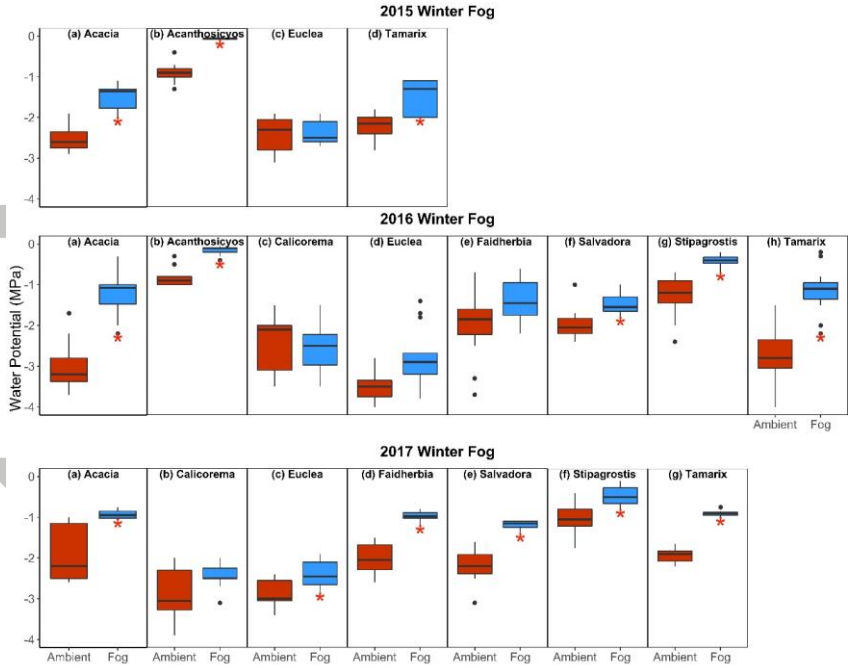

Figure 2: The effects of fog on plant water potential for *Acacia erioloba*, *Acanthosicyos horridus*, *Calicorema capitata*, *Euclea pseudebenus*, *Faidherbia albida*, *Salvadora persica*, *Stipagrostis sabulicola* and *Tamarix usneoides* in June 2015, 2016 and 2017 (winter fog). The significant plant water potential difference ($p < 0.05$) between under ambient and fog conditions was indicated by "*". In the box and whisker plots, the boundary of the box represent 25th and 75th percentile of the observations, the middle line of the box represent medians of the observations, and whiskers above and below the box represent 1.5 * IQR from the upper and lower box boundary. IQR is the distance between the first and third quartiles. The dots represent outliers outside the 1.5 * IQR.

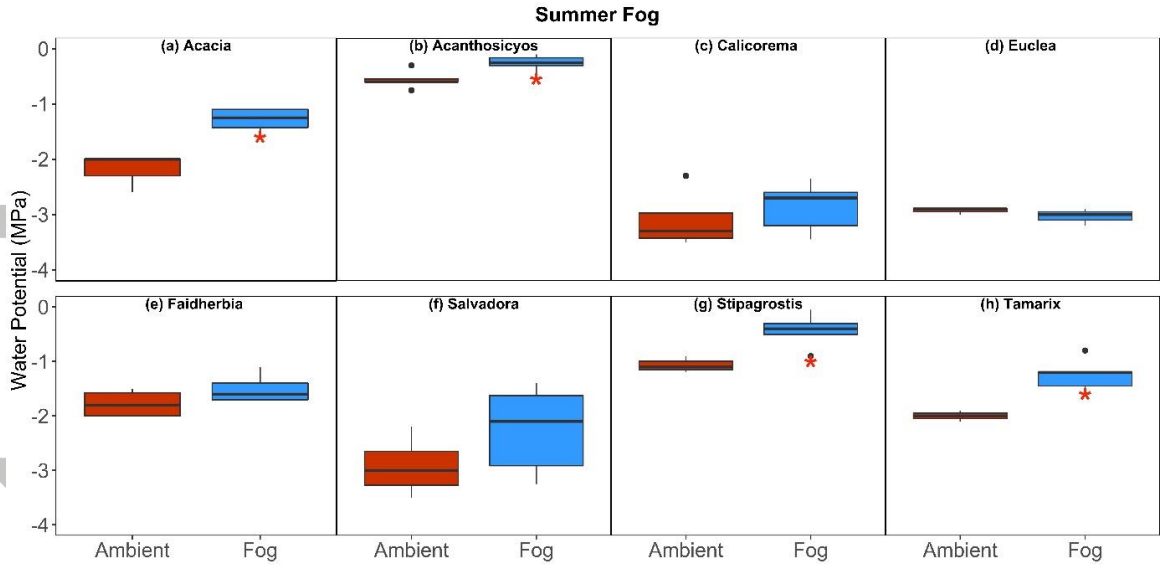

Figure 3: The effects of fog on plant water potential for *Acacia erioloba*, *Acanthosicyos horridus*, *Calicorema capitata*, *Euclea pseudebenus*, *Faidherbia albida*, *Salvadora persica*, *Stipagrostis sabulicola* and *Tamarix usneoides* in December 2016 (summer fog). The significant plant water potential difference ($p < 0.05$) between under ambient and fog conditions was indicated by "*". In the box and whisker plots, the boundary of the box represent 25^{th} and 75^{th} percentile of the observations, the middle line of the box represent medians of the observations, and whiskers above and below the box represent 1.5 * IQR from the upper and lower box boundary. IQR is the distance between the first and third quartiles. The dots represent outliers outside the 1.5 * IQR.

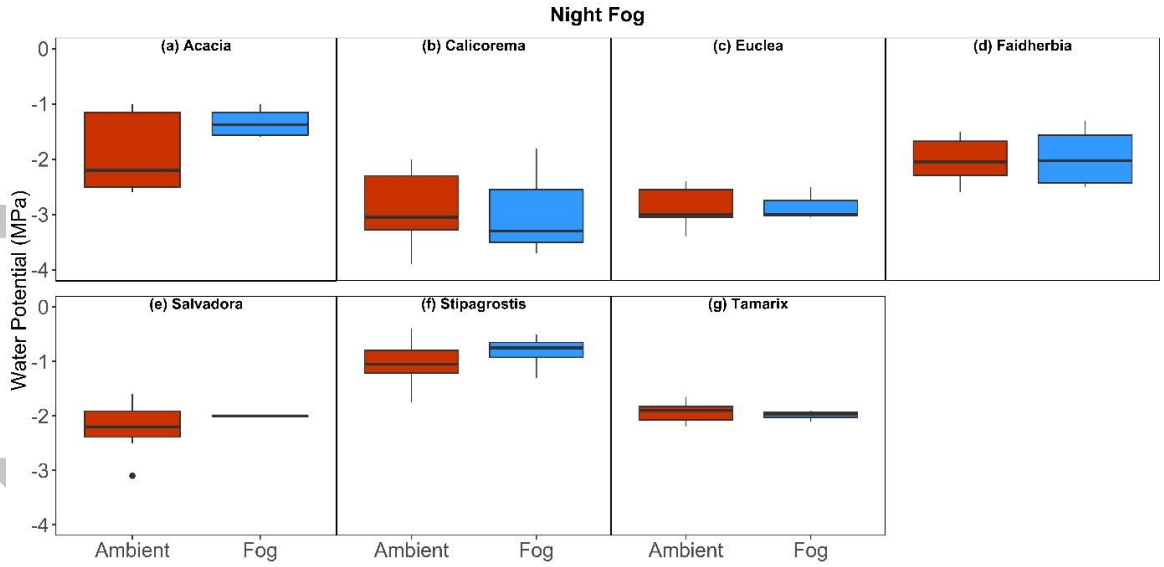

Figure 4: The effects of night fog on plant water potential for *Acacia erioloba*, *Acanthosicyos horridus*, *Calicorema capitata*, *Euclea pseudebenus*, *Faidherbia albida*, *Salvadora persica*, *Stipagrostis sabulicola* and *Tamarix usneoides* in June 2017. The significant plant water potential difference ($p < 0.05$) between under ambient and fog conditions was indicated by "*". In the box and whisker plots, the boundary of the box represent 25th and 75th percentile of the observations, the middle line of the box represent medians of the observations, and whiskers above and below the box represent 1.5 * IQR from the upper and lower box boundary. IQR is the distance between the first and third quartiles. The dots represent outliers outside the 1.5 * IQR.

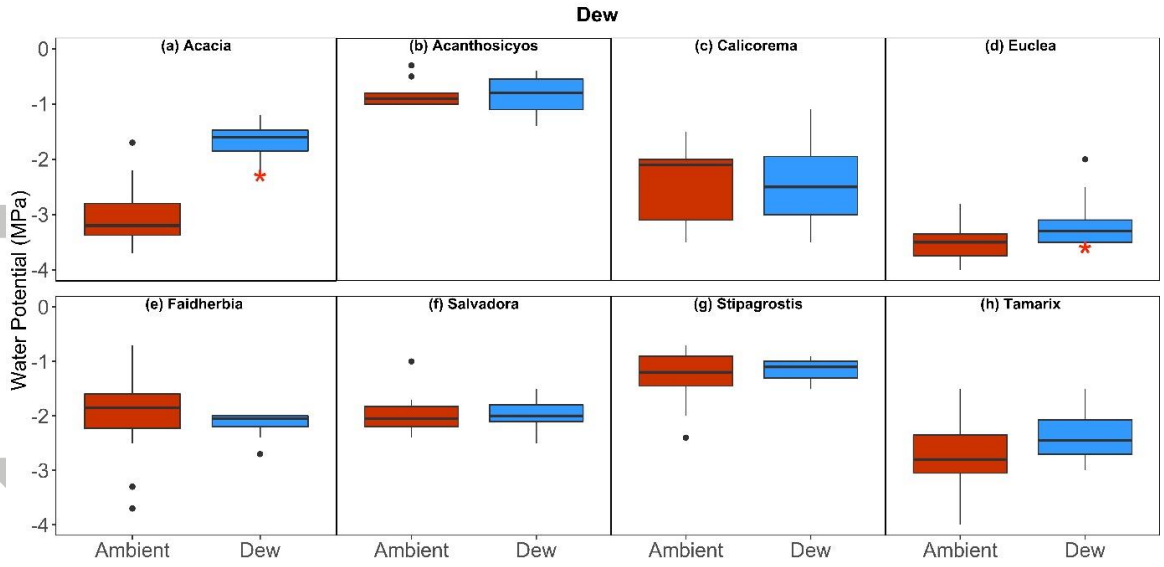

Figure 5: The effects of dew on plant water potentials for *Acacia erioloba*, *Acanthosicyos horridus*, *Calicorema capitata*, *Euclea pseudebenus*, *Faidherbia albida*, *Salvadora persica*, *Stipagrostis sabulicola* and *Tamarix usneoides* in June 2016. The significant plant water potential difference ($p < 0.05$) between under ambient and fog conditions was indicated by "*". In the box and whisker plots, the boundary of the box represent 25th and 75th percentile of the observations, the middle line of the box represent medians of the observations, and whiskers above and below the box represent 1.5 * IQR from the upper and lower box boundary. IQR is the distance between the first and third quartiles. The dots represent outliers outside the 1.5 * IQR.

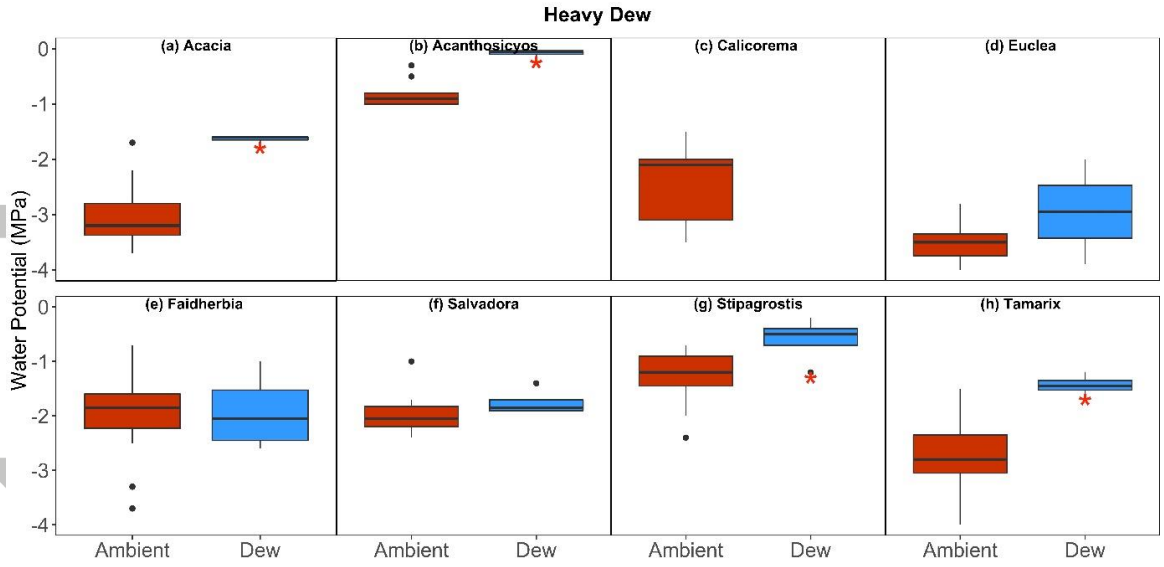

Figure 6: The effects of heavy dew on plant water potential for *Acacia erioloba*, *Acanthosicyos horridus*, *Calicorema capitata*, *Euclea pseudebenus*, *Faidherbia albida*, *Salvadora persica*, *Stipagrostis sabulicola* and *Tamarix usneoides* in June 2016. The significant plant water potential difference ($p < 0.05$) between under ambient and fog conditions was indicated by "*". In the box and whisker plots, the boundary of the box represent 25th and 75th percentile of the observations, the middle line of the box represent medians of the observations, and whiskers above and below the box represent 1.5 * IQR from the upper and lower box boundary. IQR is the distance between the first and third quartiles. The dots represent outliers outside the 1.5 * IQR.

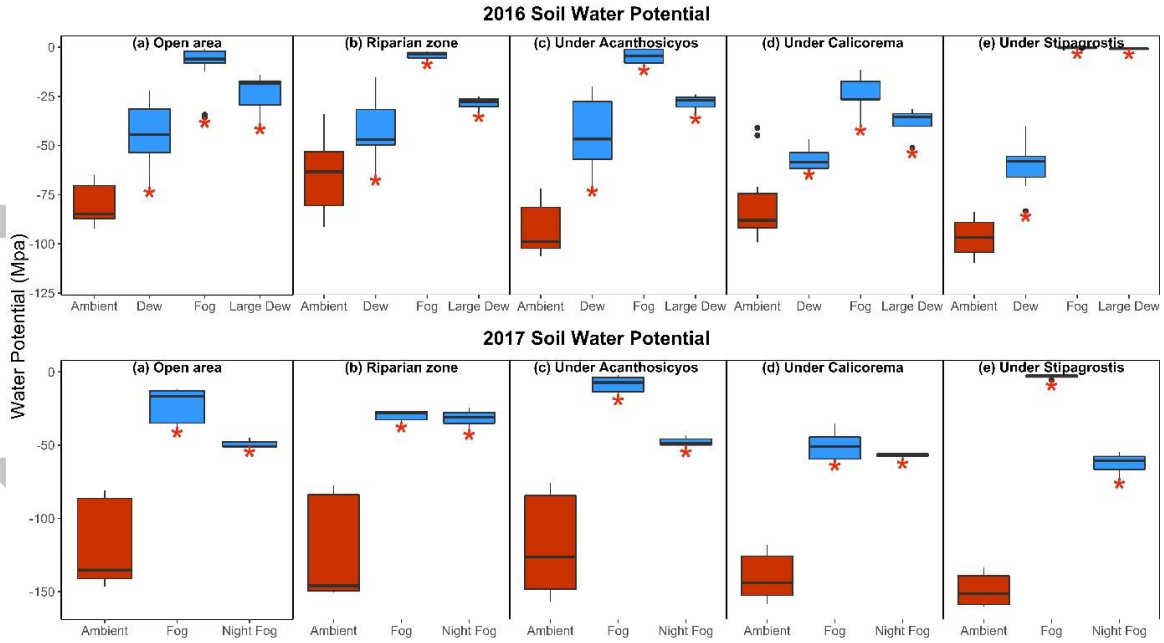

Figure 7: The effects of fog and dew on soil potentials for under open area (a), at riparian zone (b), under *Acanthosicyos horridus* (c) and under *Calicorema capitata* (d) in June 2016 and 2017. The significant soil water potential difference ($p < 0.05$) between under ambient and fog/dew conditions was indicated by "*". In the box and whisker plots, the boundary of the box represent 25th and 75th percentile of the observations, the middle line of the box represent medians of the observations, and whiskers above and below the box represent 1.5 * IQR from the upper and lower box boundary. IQR is the distance between the first and third quartiles. The dots represent outliers outside the 1.5 * IQR.

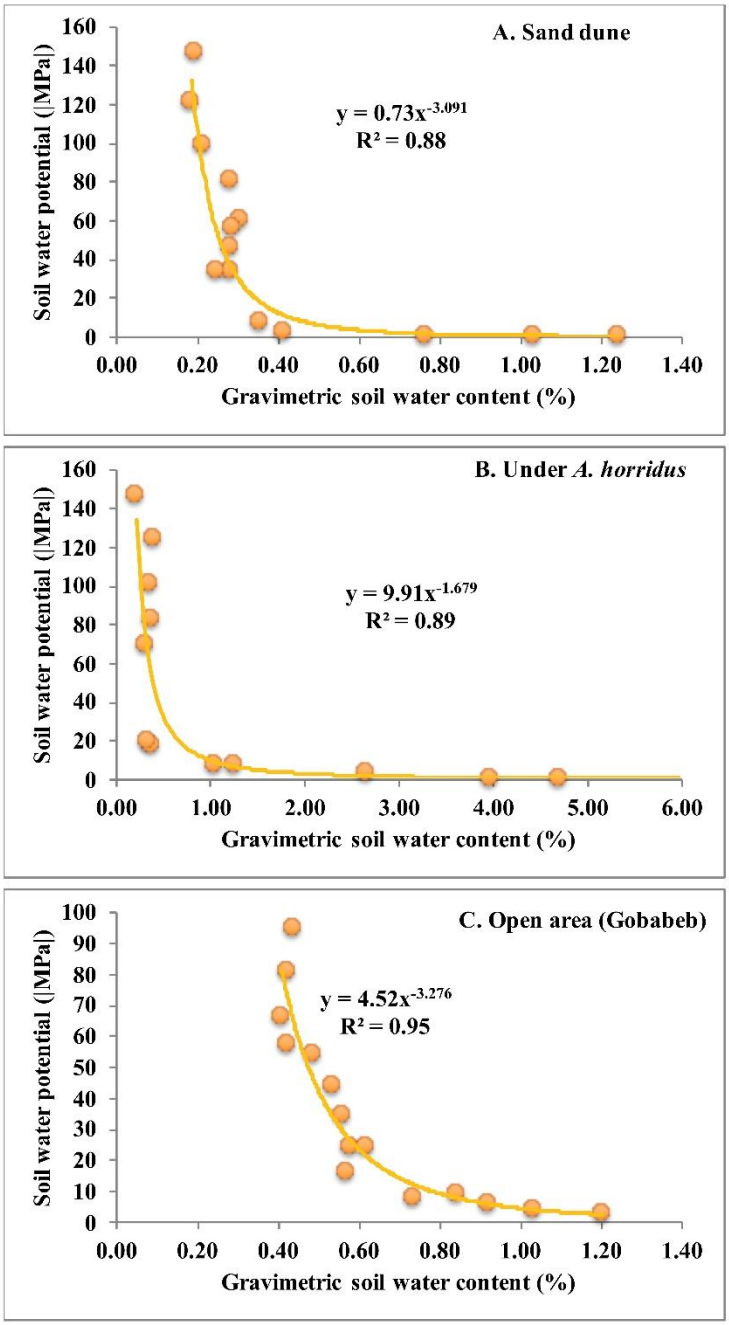

Figure 8: Water retention curves for soils from sand dunes (a), under *Acanthosicyos horridus* (b), open areas around Gobabeb (c).